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A New Heritable Color Aberration in the Tiger Swallowtail Butterfly, *Papilio glaucus* (Papilionidae: Lepidoptera)

J. Mark Scriber[1]
and
Mark Evans

Department of Entomology, University of Wisconsin, Madison, WI 53706

Abstract. A new wing color aberration in the Eastern tiger swallowtail, *Papilio glaucus* L., has been discovered and is called "dark cell". This dark scale suffusion into the dorsal forewings has a genetic basis and appears restricted to females. We describe the new aberration and our attempts to rear offspring of hand-pairings for elucidation of the genetic basis of the trait.

Introduction

A number of wing color aberrations in *Papilio glaucus* L. have recently been described by Clark and Clark (1951), Clarke and Clarke (1983) and Scriber et al. (1987). Here we report a new wing color aberration in *Papilio glaucus* L. which is apparently genetically based and sex-limited in expression. Following the first appearance of this aberration (which we call "dark cells") in our 1982 laboratory cultures, we hand-paired (sibs) in an attempt to elucidate the genetic basis of the character.

Methods

Oviposition by adult females was induced by placing each wild-captured or hand-paired female into its own clear plastic box (approximately 10 cm deep × 15 cm × 30 cm) with a moist paper towel and selected larval foodplant leaves. Leaf turgor was maintained in these plants by use of floral aquapics® (water-filled plastic vials with a rubber cap, through which leaf petioles or small branches can be inserted; see Scriber, 1977). Heat and light were provided by an incandescent bulb placed at a distance of approximately 0.3-0.5 meter from the plastic boxes.

Larvae were reared through to pupation on black cherry, *Prunus serotina* Ehrh., or another foodplant (leaves were changed three times per week) under controlled environment conditions (16:8 photo-/scotophase with corresponding temperatures of 23.5°/19.5°C, respectively).

[1]Current address: Dept. Entomology, Michigan State University, East Lansing, MI48824

Pupae were weighed 2 days after pupation (the weight subsequently serving as an identification number for the individual) and then placed in cylindrical screen cages (15 cm diameter × 12 cm height) under larval rearing conditions to permit development and eclosion as adults. Non-diapausing individuals normally emerged within 2-3 weeks after pupation. Other pupae were allowed at least 6 weeks before being refrigerated in darkness (at 40-45°F for 3 months or more) to break diapause. Hand-pairings were generally attempted 12-48 hrs after adult female eclosion and 2-3 days after male eclosion.

Results

We first observed our new color aberration in females of a 1982 lab-reared brood (#56). We term this aberration "dark cell" because of the abnormal suffusion of dark scales into the normally yellow cells of the forewings (Fig. 1). Brood #56 was the result of a yellow morph mother (a virgin *P. g. glaucus*, 3rd generation lab-reared, originally from stock collected in 1981 from Schuylkill County, Pennsylvania by William Houtz) which was mated to a male whose mother was also from this PA stock but whost father was a subspecies hybrid (from a *P. g. canadensis* female from Clarke Co., Wisconsin mated to a *P. g. glaucus* male from Pennsylvania).

Crosses #290 and #296 (Table I) are both crosses from a "dark cell" daughter and one of her male siblings (all from brood # 56). It can be seen that this dark cells trait occurs only in the females. The four siblings shown here (Fig. 1) represent some of the variation in the "dark cell" trait.

The origin of this character, and the genetic basis of its expression are difficult to decipher because of the complexity of the parental lineages, and the fact that no livestock currently exists from this lineage (brood #56, #290, or #296). Only two additional related females were hand-paired: one with a *P. g. glaucus* from Richland Co., Wisconsin (brood #299; see Table 1), and the other produced no eggs.

While checking the results of our 1982-1986 hand-pairings, lab rearings, and field captures, we discovered a total of 5 additional "dark cell" phenotypes in our research collection (> 25,000 butterflies). Each of these individuals resulted from a subspecies pairing involving a *P. g. canadensis* male parent, and each also emerged in 1984 from hand-pairings done in 1982. The first was one of 13 female progeny (19 male progeny) from a dark male *P. g. glaucus* from Georgia meted to a *P. g. canadensis* from northern Wisconsin (pairing #39). A second was one of 4 female progeny (9 male progeny) of a lab-reared yellow *P. g. glaucus* female (from Pennsylvania parents) mated to a *P. g. canadensis* from Bayfield County, Wisconsin (pairing #116). The third and fourth were female siblings out of a total of 7 females (4 male sibs) from a yellow lab-reared *P. g. glaucus* female (from Pennsylvania parents) mated to a *P. g.*

Table 1. Adult phenotypes[1] from laboratory crosses. Madison, Wisconsin (1982)

Mother number	Pairing Background (female × male)	Larvae/ total eggs	Number of Male Offspring	Number of Female Offspring "Normal" yellow	Number of Female Offspring "Dark cell"
Female #56	(#71 × #H15)	74/132	8	3	9
Female #290*	(#56 × #56)	172/391	15	8	7
Female #296	(#56 × #56)	201/271	18	1	22
Female #299	(#56 × *P. g.*)	190/208	13	6	0

[1]The "dark cell" aberration was first detected in offspring of female #56. Two fertile sibling-sibling pairings (290 and #296) both resulted in some "dark cell" phenotypes, differing from #299. One additional daughter from #56 was mated (female #537) but produced no eggs. No other pairings were made from the female #56 lineage.
*One deformed pharate female was not able to be classified.

canadensis from Juneau County, Wisconsin (pairing #144). The final "dark cell" phenotype was a female from a yellow lab-reared *P. g. australis* female from Florida, mated to a *P. g. canadensis* from Bayfield County, Wisconsin (pairing #115). Only one living pupa from these lineages currently exists.

Discussion

Sir Cyril Clarke and colleagues have been investigating the genetic basis of abnormal wing coloration in *Papilio glaucus* for decades (see Clarke and Clarke, 1983 for a review). They point out that color mosaics and gynandromorph *P. glaucus* can be striking, because of the contrast between the yellow background (of males and yellow morph females) against the black/brown melanic background of the dark morph females

Fig. 1. Four female siblings (of 22 "dark cell" produced in brood #296) exhibiting variations of our "dark cell" aberration: Left, dorsal; Right, ventral. This aberrant was originally detected in the parental brood (#56; see text and Table 1)
A) pupal weight 0.8720 g; eclosed 29 Sept. 1982
B) pupal weight 1.1946 g; eclosed 29 Sept. 1982
C) pupal weight 1,6900 g; eclosed 23 Sept. 1982
D) pupal weight 1.2956 g; eclosed 20 Sept. 1982


1A
1B
2A
2B
3A
3B
4A
4B

These dark/yellow gynandromophs and color mosaics are quite rare, and considerable attention has been given to existing specimens. For example, the Herman Strecker collection (currently on loan from the Chicago Field Museum to the Allyn Museum in Florida) contains a number of such mosaics. This valuable collection, assembled during the second half of the 19th century, contains a number of *P. g. glaucus* mosaics previously discussed in the literature (Strecker, 1878; Ehrmann, 1894; Howard, 1899; Walsten, 1977; Ehle, 1981; Shapiro, 1981b Clarke and Clarke, 1983). The Milwaukee Public Museum (Milwaukee, Wisconsin) also contains (in the Neidhoefer collection) two partial color mosaics reared by E. Dluhy in Chicago, Illinois. Color mosaics also exist from Richmond County, NY (5 July 1971; A.M. Shapiro; currently in the University of California Davis Collection) and from Washington County, PA (9 May 1927; George F. Patterson Collection at Pennsylvania State University).

Scriber and Evans (in press) describe an additional two dozen color mosaics from *Papilio glaucus* (see also Scriber et al, 1987); however, in the investigation of this entire group of color aberrations and in investigations of *Papilio glaucus* from (many) institutional and personal collections (see Scriber and Evans, 1986b), we have never encountered material similar to the "dark cell" aberration *P. glaucus* females described here (Fig. 1).

We are aware of the superficial resemblance of "dark cell" to the melanic aberration "fletcheri" in males of *P. g. canadensis*, and we have reviewed the literature and figured this form from Wisconsin previously (Scriber and Lintereur, 1983). The "fletcheri" aberration has been noted several times from northern Wisconsin (Ebner, 1960; Scriber and Lintereur, 1983; and W. Gould, J. Trick, D. Robacker, D. Matusik pers. comm.) and it is possible (though we consider it remote) that there has been introgression from our handpairing with *P. g. canadensis* in the lineage leading to the male parent of brood #56. It should be noted however that the "fletcheri" aberration is generally believed to be restricted to the male, and apparently to *P. g. canadensis*. Furthermore, "fletcheri" exhibits significant suffusion of dark scales into both the hindwings and forewings, with an orange smear encroaching ventrally as well as dorsally across the hindwings (see color figure in Scriber and Lintereur, 1983). Our "dark cell" aberration is essentially restricted to the forwings, and only their dorsal surface (Fig. 1).

We do not necessarily mean to imply that the "dark cell" trait (restricted to females) can not be genetically related to the "fletcheri" aberration (apparently restricted to males). In fact, we know that sex-linked (female Y-chromosome) control of the dark morph color polymorphism in *P. glaucus* females (Clarke and Sheppard, 1962) can be transmitted by males in what we consider to have been either a crossover event or a non-disjunction (Scriber and Evans, 1986). The role of *P. g. canadensis* introgression in these events is unclear, but such

gene flow between the two subspecies can be disruptive in a number of ways to other morphological/color traits (Scriber, 1982; Luebke, 1986; Rockey et al, 1987; Scriber, 1987). Unfortunately we will be unable to conduct any further studies of this now extinct "dark cell" lineage.

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Literature Cited

CLARK, A. H. & L. F. CLARK. (1951) The butterflies of Virginia. Smithsonian Institute Miscellaneous Collection, 116(7), 124-144.

CLARKE, C. & F. M. M. CLARKE (1983) Abnormalities of wing pattern in the eastern tiger swallowtail butterfly *Papilio glaucus*. Systematic Entomology, 8, 25-28.

CLARKE, C. A. & P. M. SHEPPARD (1962) The genetics of the mimetic butterfly, *Papilio glaucus*. Ecology 43:159-161.

EBNER, J. A. (1960) A striking melanic male of *Papilio glaucus*. J. Lepid. Soc. 14:157-158.

EDWARDS, W. H. (1868) Notes on a remarkable variety of *P. turnus* and descriptions of two species of diurnal Lepidoptera. Trans. Amer. Entomol. Soc., 2, 207.

EDWARDS, W. H.(1884) Butterflies of North America. Vol. II. Philadelphia Houghton Mifflin Co.

EHLE, C. (1981) Letter to the editor. News of the Lepidopterist's Society (No. 5, Sept./Oct.), p. 63.

EHRMAN, G. A. (1893) A few remarkable variations in Lepidoptera. Canadian Entomologist, 26, 292-293.

HOWARD, L. O. (1899) An abnormal tiger swallowtail. Insect Life, 7, 44-47.

LUEBKE, H. J. (1986) Hybridization in the *Papilio glaucus* group: A morphometric study using multivariate techniques. M. S. Thesis, Univ. Wisconsin, Madison. 102 pp.

NIJHOUT, H. F. (1981) The color patterns of butterflies and moths. Scientific American. November: p. 140-151.

ROCKEY, S. J., J. H. HAINZE, & J. M. SCRIBER. (1987) A latitudinal and obligatory diapaus response in three subspecies of the Eastern Tiger Swallowtail, *Papilio glaucus* (Lepidoptera: Papilionidae): Amer. Midl. Naturalist (in press).

SCRIBER, J. M. (1982) Foodplants and speciation in the *Papilio glaucus* group. pp. 307-314 *In* Proc. 5th Intern. Symp. Insect-Plant Relationships. Pudoc, Wageningen.

SCRIBER, J. M. (1987) Tale of tiger: Beringial Biogeography, bionomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies. IN: Chemical Mediation of Coevolution (K. C. Spencer, ed.) (submitted Dec. '85). (in press, AIBS).

SCRIBER, J. M. & M. H. EVANS. (1986) An exceptional case of paternal transmission of the dark form female in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae) Journal of Research on the Lepidoptera (25: in press).

SCRIBER, J. M. & G. L. LINTEREUR (1983) A melanic aberration of *Papilio glaucus canadensis* from northern Wisconsin. Journal of Research on the Lepidoptera 21: 199-201.

SCRIBER, J. M., M. H. EVANS & D. RITLAND (1987) Hybridization as a causal mechanism of mixed color broods and unusual color morphs of female offspring in the eastern tiger swallowtail butterflies, *Papilio glaucus*. *In* (M. Huettel, ed.) Evolutionary Genetics of Invertebrate Behavior. Univ. of Florida (in press).

SHAPIOR, A. M. (1976) Seasonal polyphenism. Evolut. Biol. 9:259-333.

SHAPIRO, A. M. (1981b) Letter to the editor; Ripples. News of the Lepidopterists' Society (Jan.-Feb., No. 1, p. 5).

STRECKER, H. (1878) Butterflies and moths of North America. Owen Press, Reading, PA. 280 pp.

WALSTEN, D. M. (1977) Letter to the editor; Ripples. News of the Lepidopterist's Society (Sept.-Oct., no. 5, p. 6).

VANE-WRIGHT, R. I. & P. R. ACKERY. 1984. The biology of butterflies. Academic Press, London.